The dancing queen: explanatory mechanisms of the 'feel-good-effect' in dance

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The dancing queen:
Explanatory mechanisms of the 'feel-good-effect' in dance

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Abstract

Dance is a social, creative form of human activity that impacts on one's wellbeing as a result of the emotions involved in active or passive participation or the opportunity to achieve high levels of mastery and professional fulfilment. Further, dance as a form of physical activity has the potential to improve health in its physiological dimensions in addition to the psychological and social aspects. Although in recent years we have witnessed a surge in dance-related research, this area of human behaviour is still relatively unexplored. Therefore, in the present chapter we explore possible mechanisms that may contribute to the "feel-good-effect" of dance participation by emphasising its positive as well as potentially detrimental effects through the understanding of the physical activity literature as a starting point. We address biochemical, brain neurotransmitters, and psychological mechanisms that are thought to explain the impact of physical activity in wellbeing and we will discuss functional and structural brain changes that were linked to participation in dance. We conclude by highlighting the need to increase overarching research efforts in order to better recognise the potential risks and benefits of dance in improving health and wellbeing.

Keywords: Brain, cognitive neuroscience, exercise, neurotransmitters, physical activity, social connectedness, wellbeing.

Introduction

Over the last decade, an increasing number of research publications have shown evidence for positive effects of dance participation on individuals' health and wellbeing across a large spectrum of age groups and societies (Gardner et al. 2008; Keogh et al. 2009; O'Neill et al. 2011). The positive effects include a strengthening of group coherence, an increasing willingness to help others, an improvement of successful rehabilitation (see Quiroga Murcia, Kreutz, Clift, & Bongard, 2010) as well as accident prevention (Fernandez-Arguelles et al. 2015). The rise in empirical investigations into the benefits of dance is surprising: dance is still frequently stigmatized as a low-level leisurely activity on the one hand (e.g., Walker 2010) and as an unhealthy profession on the other hand (e.g., Koutedakis & Sharp 1999). Moreover, dance professionals have been socially and intellectually denounced well into the 20th century (Garfola 2010). Based on myths associated with dance such as these, many sceptics do not even consider dance as a profession per se.

However, with an emphasis on dance as a form of physical activity and the surge to find solutions to reduce obesity and other health-related issues that are based on the populations' increasing physical inactivity, dance offers great opportunities. Notably, dance is a very popular joyful activity to do as well as to watch. It is only second to football as the most commonly offered physical activity in UK Schools' physical education curriculum. In addition, school links to clubs showed the biggest increase for dance since 2008 (Quick et al. 2010). Nevertheless, for a successful implementation of dance interventions, it is important that dance overcomes the stigma attached to it; predominantly those regarding age, class, race, gender, level of physical activity and appearance.

According to Lansley & Early (2011, p. 12), ageism is the most critical prejudice in dance as it affects dance hardest and often remains unvoiced. Due to physical and psychological demands, dancers' careers are understood to be extremely short (e.g., Wanke et al. 2012). However, recent trends provide encouragement that performing dance is possible at a higher age (e.g., Pina Bausch, Sylvie Guillem, Carlos Acosta, Tamara Rojo, Steve Paxton, Jane Dudley, Julyen Hamilton, see also Figure 1). Furthermore, with mature dancers becoming increasingly present, the possibilities when defining goals and designing appropriate training schedules for dancers at different levels and stages are more tangible.

[INSERT FIGURE 1 and LEGEND 1 ABOUT HERE]

Another poignant misconception of and in dance is related to the intensity and level of physical activity in dance. With so many different dance styles, the intensities of the physical demands are almost impossible to summarise and dance-specific knowledge is required to recognise the demands on dancers' bodies (Wanke et al. 2012). Notably, while the cardiovascular and muscular efforts dance demands may be discredited by some, professional dancers are expected to have a mind-set of 'never giving up' which poses risks for health and wellbeing.

Clearly, professional dance expertise is a highly trained skill achieved through a huge amount of deliberate practice (Ericsson, 2008). However, recent research conducted at top UK Universities (e.g., Laban Trinity College, Royal Holloway) provided evidence that tailored high intensity training programmes should include resting periods for optimal dance performance and injury prevention and focus on quality, not quantity (Wyon, 2010). The importance of rest periods for consolidation processes of general complex motor (Rieth et al. 2010) and cognitive tasks (Mercer 2014) is an established fact. It is thus important that pauses in dance practice are credited. Wyon (2010) for example, suggested that a rehearsal can end early, particularly when the desired quality is achieved. For most professional and vocational dancers, this, however, is not common practice.

De facto, it is often the case that insights that go against existing cultural practices are particularly slow in being implemented. This is true for dance with its prejudices and expectations, as well as with science with its established empirical standards. For example, while the amount of research on the physical, psychological and neuronal processes linked to dance increased tremendously over the last decade, the predominantly reductionist scientific approach has often failed to capture the complexity of dance (Jola et al. 2012; Jola in press) and interpretations need to be handled carefully. We argue that with a better understanding of the underlying physical, neuronal and psychological mechanisms of dance, more substantial critique of existing practices and better targeted propositions for novel approaches in support of health and wellbeing in dance are possible – even if some of these scientists may not have initially set out to target those aspects (e.g., Cross et al. 2014)

In general, physical activity has been associated with a variety of health benefits including a sense of feeling good (Haskell et al. 2007; Penedo & Dahn 2005; Warburton et al. 2006). This "feel-good-effect" associated with physical activity is linked to physiological as well as psychological effects (Ekkekakis, 2003; Hyde et al. 2011). Notably, positive effects through dance participation can be expected to go beyond physical health since dance in its optimal form combines physical activity with cognitive, social, psychological (including emotional), spiritual, and creative processes (e.g., Burkhardt & Rhodes 2012; Siddall 2010). Indeed, dance participants reported beneficial effects on all of these factors (Quiroga Murcia et al. 2010) with a more positive-activated (e.g., feel happy, elated, energetic, euphoric) as well as more positive-deactivated (e.g., feel released, relaxed, calm) feeling after dancing. Furthermore, quantitative studies found positive effects of recreational dance interventions on physical and psychosocial health and wellbeing in children and adolescents (Burkhardt & Brennan 2012) as well as in the older population (Connolly & Redding 2010).

While there is considerable consensus in what pertains to the health and wellbeing benefits of physical activities in general, the research concerning the explanatory mechanisms of such benefits is less conclusive. This chapter thus aims at initiating a pathway towards a more comprehensive understanding of the underlying mechanisms of the benefits of dance as a special form of physical activity. We emphasise the physical activity component of dance to the detriment of other, nonetheless relevant, components (e.g., see Christensen & Jola 2015; Jola in press) because of (a) the contemporary political relevance of viewing dance as a physical activity and (b) the need to understand mechanisms of health and wellbeing that underpin the physical aspects of dance.

We argue that a better understanding of the complexity and interaction of these explanatory mechanisms will provide substantial support for the successful continuation of dance participation with a focus on health and wellbeing. This is particularly important since dance also entails considerable health and wellbeing risks (e.g., Padham & Aujla 2014) in addition to the high risk of dance specific physical injuries (e.g., Russell 2013). In the professional, vocational and sometimes recreational sectors, high incidences of injuries, fatigue, and psychosocial pressures are prevalent, potentially leading to distorted eating habits (e.g., Aalten 2007), continuous practice despite serious injuries (e.g., Nordin-Bates et al. 2011), and escapes into drug misuse (e.g., allegations in the Danish newspaper on the drug misuse at the Danish Royal Ballet; see also Sekulic et al. 2010). According to some authors, the most prevalent risk factors are of cultural and aesthetic origin (see Aalten 2007, Wanke et al., 2012). For example, ballet dance defies gravity and the anatomy of the human body, causing stress on the dancer’s body and mind (see also Wyon et al. 2011). Thus, concerns about professional and vocational dancers’ health and wellbeing are understandably high and its potential effects on the recreational sector should not be ignored. The aim is therefore to sensitise the reader to the characteristic effects of dance practice that allows a more informed understanding of often contradicting findings.

Explanatory Mechanisms

Among the various hypotheses advanced to explain a relationship between physical activity and wellbeing in dance, we emphasise the biochemical, neuronal and psychosocial mechanisms. Notably, while some of the explanatory mechanisms in relation to dance have been studied extensively (e.g., psychosocial effects of dance movement therapy or self-perception, functional brain changes), others have received little attention (e.g., structural brain changes, neurohumoral and serotonin/dopamine responses; but see Quiroga Murcia et al. 2009). Hence, for those cases where no specific reference to dance is available, we report from a general physical activity/exercise perspective and discuss potential links to dance practice to stimulate further research.

Biochemical mechanisms

The endorphin hypothesis

Endorphins such as β-endorphins, encephalins and dynophin are hormones that have an important role in the regulation of pain perception and feelings of euphoria. Due to its analgesic effects, these opioid peptides can mediate psychological benefits of physical activity; it has been suggested that the increase of circulatory endorphins, particularly β-endorphins, observed during physical activities is responsible for the "runner's high", so often reported by regular joggers (Marieb 1995).

Presently, evidence for the increase of plasma level endorphins exists in relation to the increasing effort demands of the activity in anaerobic exercise (e.g., Schwarz & Kindermann 1992), aerobic dance (Pierce et al. 1993), and the interactivity of the movements with music (Tarr et al. 2014). Whether the anaerobic threshold is reached in dancing or not, is dependent on the dance style (Angioi et al. 2011; Liiv et al. 2014; Wyon et al. 2011). Also, not music listening per se, but the creation of music and interaction with music was shown to determine endorphin release (Dunbar et al. 2012). For example, interactive musical feedback during a repetitive machine supported workout was found to enhance the individuals' mood compared to passive music listening (Fritz et al. 2013). In addition, Tarr et al. (2014) proposed that agency and/or group co-ordination are necessary for music-induced endorphin levels to rise. These findings support the notion that during dance practice, live music should be preferred over recorded music and that dancers release more endorphins – even when the dancers may not reach the anaerobic threshold – when a communicative interaction between performers and the musician is present.

It is less clear, however, whether the feeling of "high" after performing could be induced by endorphins. To our knowledge, only one study addressed the endorphin response specifically to dance (Pierce et al. 1993) showing an increase of circulating endorphins after 45 minutes of aerobic dance. However, the endorphins are unlikely to be directly responsible for the "feel-good effect" in dance as well as other physical activities: although blood concentration of endorphins is generally increased during exercise, its effects on mood states are questionable. Researchers have failed to demonstrate that endorphins are able to pass through the blood-brain barrier to act on the brain centres responsible for the regulation of mood (Boecker et al. 2008; Buckworth et al. 2013; O'Neal et al. 2000). However, Boecker et al. (2008) were the first to show *in vivo* evidence in human participants that sustained physical exercise resulted in release of endogenous opioids (within the central nervous system) in the fronto-limbic regions of the brain (see Figure 3), responsible for affective modulation. More importantly, such increased opioid activity was associated with the euphoric sensation characteristic of the "runner's high". Further investigations are required into studying how mood in recreational and professional dancers may depend on endogenous opioid levels. Although these are associated with wellbeing as discussed, it may also explain the possible "exercise addiction" observed in injured professional and recreational dancers

(Nordin-Bates et al. 2011) and athletes alike (Boecker et al. 2008); who continue their training regardless of the harmful consequences to their health. Nevertheless, it appears that the feeling of “high”, particularly experienced after performance, is more likely related to cortisol levels.

Dance and cortisol response

As represented in Figure 2, the hypothalamic-pituitary-adrenal (HPA) axis regulates the stress response of an organism, ultimately through the liberation of a number of hormones such as cortisol. Exercise has been shown to influence the HPA system that regulates stress responses. While “acute” exercise activates this system, adaptation to repeated bouts of exercise (“chronic” exercise) attenuates the effects of acute exercise regardless of its intensity; therefore, repeated exercise results in decrease HPA activation (Buckworth et al. 2013). Hence, as a form of physical activity, regular dance can have a beneficial impact on wellbeing through the regulation of the HPA axis activation.

[INSERT FIGURE 2 ABOUT HERE]

Although exercise is a physical strain that can activate the HPA axis, particularly in episodes of intense physical exertion (Davis & Few 1973; McMurray et al. 1996; Tremblay et al. 2005), the psychological demands of the stimuli can activate the HPA axis more strongly than the physical demands (Berndt et al. 2012; Rohleder et al. 2007).

Increases in positive affect and decreases in salivary cortisol concentrations were found in a sample of tango argentine dancers (Quiroga Murcia et al. 2009). Specifically, regular dancing (with partner and music) resulted in lower levels of cortisol than dancing with partner without music. In addition, music also had an influence on the neurohumoral responses to dance as significant decreases were observed in tango dancing with music but without a partner. Conversely, elevated cortisol levels were also found in competitive ballroom dancing (Rohleder et al. 2007) and dance students during short solo performances

(Quested et al. 2011). Notably, these changes were shown to occur due to the social-evaluative threat associated with the competitive nature of the tasks rather than the physical exertion required. Berndt et al. (2012) argue that professional dancers are subject to a variety of stressors that may result in acute increased cortisol responses that when repeated over a long period of time (i.e., chronic stress exposure) can lead to loss of quality of life associated to enhanced stress sensitivity, pain and fatigue.

Quested et al. (2011) argues that the positive effect of dance on wellbeing can be due to fulfilment of individuals' basic psychological needs, that is, the need to feel competent, in control of own behaviour and socially connected with others (Ryan & Deci 2000). Quested et al. (2011) found evidence that low levels of satisfaction of dancers' basic psychological needs may result in prolonged or repeated cortisol elevation, which can have negative consequences on long-term wellbeing (Burns 2006). Dancers who reported higher basic psychological needs satisfaction had lower cortisol responses and anxiety intensity. In addition, Rohleder et al. (2007) demonstrated lower cortisol levels in group formation dancers in comparison to individual couple dancers, which the authors attributed to the social support experienced during the group dancing. These results demonstrate that the psychological satisfaction is crucial for dancers' health and wellbeing; potentially more so than the type or level of physical exertion while dancing.

Brain neurotransmitters

Whether physical, social or psychological the aetiology, there is a documented association between physical activity and exercise with an enhancement of the transmission of brain chemical neurotransmitters, specifically dopamine, norepinephrine and serotonin (Hyde et al. 2011). Notably, the study of changes in brain neurotransmitters following exercise relies primarily on animal models (Dishman 1997).

Dopamine (DA) has an important role in initiating and controlling movement (Meeusen & De Meirleir 1995). Habitually physically active animals have an enhanced brain DA synthesis (Foley & Fleshner 2008) and DA metabolism in the brain as a whole (Chaouloff 1989) or in specific regions (see Figure 3) such as the midbrain, hippocampus, striatum, and hypothalamus (Davis & Bailey 1997). Exercise affects the dopaminergic system, for fatigue was associated with reductions of DA synthesis and metabolism in the brain stem and midbrain. Furthermore, when brain DA levels were maintained, fatigue was delayed.

Notably, dopamine is also one of the regulators of appetite (Abizaid 2009). Therefore, the increased dopaminergic activity after the intense physical exertion associated with professional dance practice could explain the experience of dancers in suppression of their appetite (Crabtree et al. 2014). In combination with aesthetic or schedule enforced diets (e.g., Aalten 2007; Koutedakis & Jamurtas 2004), these exercise induced appetite suppressions can lead to detrimental effects on the individual’s health, that have not yet been systematically researched (Howe et al. 2014).

Moreover, empirical studies that specifically target dancers’ nutritional needs are to this day marginal but much needed. For example, Brown and Wyon (2014a) showed evidence that dancers’ positive mood is significantly linked to their nutrition behaviour and blood sugar, i.e., glucose, levels. The authors’ also showed that attempts to educate dancers on the nutritional needs potentially in form of supplements are important (Brown & Wyon 2014b). Clearly, more field studies are needed to gain a better understanding of the specific needs and problematic issues (such as increased proneness to injury due to inadequate diet, see Wanke et al. 2012) related to changes in biochemical mechanisms and nutritional modifiers of the feel-good effect.

Norepinephrine (NE) is a major modulator of neural activity in the brain (Dunn & Dishman 1991) and the primary brain site for its production is the *locus coeruleus*, located in the pons (Buckworth et al. 2013, see Figure 3). Noradrenergic responses regulate autonomic arousal, attention-vigilance, and neuroendocrine responses to stress (Dishman 1997), including those associated with anxiety and depression (Soares et al. 1999). Studies suggest that chronic physical activity alters brain levels of NE and its major metabolites in regions of the brain known to be involved in integrating behavioural and endocrine responses to stressors other than exercise (Dishman 1997; Sothmann & Kastello 1997). Research also suggests that in physically active animals there was less NE depletion or higher synthesis rates during exposure to controllable and uncontrollable stressors when compared with sedentary animals (Dunn et al. 1996). Furthermore, research also suggests the role of exercise in increasing brain NE activity in conditions of chronic hypoadrenergic activity (Sothman & Kastello 1997), by providing “psychopharmacological evidence consistent with an anti-depressant effect of physical activity” (Dishman 1997, p.67). In fact, chronic activity-wheel running protected against the depletion of NE in face of stressors (e.g., uncontrollable foot-shock) in sedentary animals (Dishman et al. 1997; Dishman et al. 1993; Soares et al. 1999).

Serotonin (5-HT) neurons are distributed to all areas of the central nervous system. Activity of 5-HT neurons is associated with pain, fatigue, appetite, sleep, and corticosteroid activity (Dunn & Dishman 1991). Levels of 5-HT or its metabolite, 5-hydroxyindoleacetic acid (5-HIAA), in the cerebrospinal fluid and urine are below normal during depressive episodes in humans (Landers & Arent 2001). Although research that focused on the effects of exercise on the serotonergic system has generated mixed results (Dunn & Dishman 1991), there is some evidence that exercise increases brain 5-HT synthesis and metabolism (Chaouloff, 1989; Davis & Bailey 1997). Analysis of regional differences in 5-HT and 5-HIAA following 90 minutes of treadmill running showed increases of both substances in the midbrain, hippocampus, and striatum (Davis & Bailey 1997, see Figure 3). Such increases are thought to be facilitated by improved concentration of free tryptophan levels in the blood after exercise, which stimulates tryptophan entry in the brain for 5-HT synthesis (Chaouloff 1997; Meeusen & De Meirleir 1995). Chaouloff (1997) showed that one hour of treadmill running resulted in increased brain tryptophan concentration accompanied by a small but significant increase in 5-HIAA, indicative of increased 5-HT synthesis and turnover.

In addition to the focus on brain monoamines in animal models, studies of the presumed anxiolytic effects of exercise focussed on increased locomotion, which reflects an adaptive motivational state indicating reduced behavioural inhibition (e.g., few approaches to the centre of the open field, freezing) (Dishman 1997). Fearful locomotion is regulated through reciprocal inhibition between gamma aminobutyric acid (GABA) and dopamine transmission within the corpus striatum (Dishman et al. 1996). The corpus striatum is a set of nuclei located in the forebrain, responsible for the coordination of slow sustained body movements, and inhibition of unnecessary movement patterns. Consistent with the suggestion that exercise has an anxiolytic effect in rats, Dishman et al. (1996) observed that chronic activity-wheel running increased locomotion during open field behaviour and decreased the density of $GABA_A$ receptors in the corpus striatum subsequent to increased GABA concentration.

Animal studies have showed that environmental manipulations such as exercise induced biochemical changes that have been found to mediate the antidepressive benefits observed by pharmacological treatments (Remington 2009). However, studies with humans are limited for technical and ethical reasons making measurement of brain neurotransmitters difficult. For example, in a rare study performed with humans, Wang et al. (2000) did not detect any changes in DA striatal release after 30 minutes of vigorous aerobic exercise on the treadmill. The authors attributed this failure to corroborate the research with animal studies to the poor sensitivity of the method used to detect low levels of DA increase. Therefore, studies focus mainly on peripheral levels of these catecholamines. Plasma levels of norepinephrine and dopamine were found to be increased after both moderate and intense bouts of physical exercise (Winter et al. 2007). Jeong et al. (2005) have identified increases in plasma serotonin concentration and decreases in dopamine concentration in adolescents with mild depression following 12 weeks of dance movement therapy (DMT).

In summary, because monoamines contribute to the adjustment of the activity of the thalamus and limbic system (see Figure 3), responsible for the regulation of mood states and emotional functioning (Buckworth et al. 2002), the possibility that exercise may stimulate production and release of monoamines in the brain may justify the preventive and therapeutic role of exercise (Biddle & Mutrie 2008) and as a consequence this of dance.

Neuronal mechanisms

Background dance and the brain

As figure 3 illustrates, the outer surface of the brain is divided into four main lobes. These lobes entail formations called gyri and sulci, which are used to identify the lobes. In analogy to landscape, the gyri and sulci would be the ‘hills’ and ‘valleys’, respectively. En gross, the different lobes are found to process different types of information. For example, the occipital lobe processes visual information, the temporal lobe auditory information, the parietal lobe spatial and physical properties, and thinking has been located in the frontal lobe. The more inferior structures are considered to process emotional information. While there is good reason to assume a close relationship between functional processes and the underlying neuronal architectures, to assume such a distinct modular structure of the human brain is a tremendous simplification. The cognitive and perceptual processes are complex, depend on several parts of the brain, and are inevitably interlinked, leading to a network of activity across the brain when conducting a task. In the case of dance, it is important to understand that the brain's activity spans across an extended network of areas involved in the processing of multiple sensory, motor, cognitive and emotional functions.

[INSERT FIGURE 3 ABOUT HERE]

These diverse ranges of functions are 'orchestrated' in the grey matter, the outer layers of the cortical surface, consisting of nerve cells. The underlying white matter contains connections between nerve cells, mostly myelinated axons. Here, our main interest is in how a dancer's brain adapts to its demands and how this may explain some of the effects on health and wellbeing.

Adaptations to environmental inputs as well as internal modulations are an intrinsic property of the human brain (Pascual-Leone et al. 2005). Novel techniques, such as magnet resonance imaging (MRI), electroencephalography (EEG) or near infrared spectoscropy (NIRS), allow assessing such neuroplasticity non-invasively, in form of changes in brain function (activity of grey matter in response to particular stimuli or tasks) and the brain's architecture (structural anatomy of grey and white matter). Notably, however, each method has its particular limits. For example, measuring brain activity during large whole body movements presents a challenge due to movement artefacts. Moreover, the narrow space in an MRI scanner poses an undeniable adversity when aiming to study activity in response to dance.

Other restrictions are the spatial and temporal resolutions of each method (Logothetis 2008). The vast amount of neuroscientific studies on dance published over the last ten years has predominantly looked at functional brain processes in the domain of perception and cognition in response to dance practice without considering accompanying structural differences (Blaesing et al. 2012; Sevdalis & Keller 2011). Direct links between functional and structural changes in so-called 'motor training-induced neuroplasticity' (Bezzola et al. 2012) have yet received limited attention. Notably, in particular for health and wellbeing

(Bolandzadeh et al. 2012) as well as brain changes based on learning and expertise (Fields 2010), the white matter structure is nonetheless important.

Nevertheless, studies that acknowledge dance in its full complexity (i.e., high ecological validity) as an audio-visual stimulus that contains multiple sensory practices impacting on vision, audition, touch, and somatosensory processes have increased in number. This led to an even stronger presence of dance in science with advancing interdisciplinary approaches and novel methodologies. This interdisciplinary approach is important because, as discussed above, the multiple sensorial aspects of dance (i.e., movement and music) are vital for health and wellbeing benefits of dance.

Functional Changes – Mirroring and Empathy

The main body of the early research on dancers' functional brain changes predominantly investigated neuronal processes of passive action observation. This research was in particular stimulated by the finding of the so-called 'mirror neurons' in the macaque monkey's frontal and parietal brain areas (Rizzolatti et al. 1996). The authors made the coincidental finding that neurons in the area relevant for motor execution (e.g., when the monkey grasped a piece of food) were also activated when the monkey passively observed an action (e.g., when the monkey observed the experimenter grasping food), as if internally "mirroring" or simulating the observed action and thus potentially building the basis for understanding others and experiencing empathy.

An interesting means to study these mirror neurons is dance. Dance is an universal phenomenon, developed to a variety of cultural forms, with movements ranging from object-unrelated gestural to fully abstract actions. These characteristic properties allow studying action observation in refined forms. For example, comparing brain activity of spectators with different levels of physical and visual expertise in different styles of dance advanced our understanding of the role of context effects in abstract as well as gestural dance movements

(Jola, Abedian-Amiri et al. 2012; Jola et al. 2013; Jola & Grosbras 2013). Largely, action observation studies with dancers showed that brain activity is dependent on physical familiarity with the observed movements. In other words, dancers who watched movements that closely matched the movements they master, showed enhanced activity in areas considered part of a mirror neuron system (see Figure 3), also described as the action observation network (e.g., Calvo-Merino et al. 2005; 2006; Cross et al. 2006).

Specific roles have been associated with the different parts of the mirror neuron system. The primary motor cortex is relevant for the motor action, the superior temporal sulcus - considered lacking motor execution functions (Rizzolatti & Craighero, 2004; but see also Gazzola & Keysers, 2009) - is relevant in the perception and recognition of a human body (see Noble et al., 2014) and thought to further process the visual properties of motor actions (Werner et al., 2012). While the parietal lobe has been described frequently as part of the mirror neuron system, its superior parts are more likely related with the preparation to imitate an action (Cattaneo & Rizzolatti, 2009). Finally, the role of the inferior frontal gyrus has just recently been associated with the processing of complex movement structures (e.g., Noble et al. 2014; Bachrach et al. under review). Further, the somatosensory cortex is the part of the brain that is involved in the sensation of motion, or in the case of passive action observation, it signifies "how the action would feel if executed" (Gazzola & Keysers, 2009)[1].

It is interesting to note that one would expect dancers to engage particularly in the sensation of movements. Although dancers indulge in kinaesthetic pleasures of movements and potentially employ somatosensory information in lieu of visual information (e.g., Ehrenberg, 2010; Jola et al. 2011), the somatosensory cortex activity was not consistently

[1] Though it must be noted that Gazzola and Keysers (2009) contrasted brain activity within each individual participant during the execution of an action with the observation of the action. This is an appropriate approach to assess mirror-neuron activity. Notably though, it is in contrast to most studies involving dancers, most of which only measured brain activity during passive action observation (one exemption is the study by Brown et al. 2006, who measured tango dancers' brain activity during dancing steps using PET).

identified in studies designed to test the mirror neuron theory. Sensory experiences evoked through dance as well as the influence of context related elements (e.g., watching with or without music as in Jola et al. 2013) have been studied less. Hence, the seemingly obvious link between dancers' health and wellbeing (enjoyment) and activity in their neuronal action observation processes (enhanced somatosensory activity) may have been missed. In fact, since neuroscientific studies often neglected the rich variety of dynamic gestures in dance by defining dance along the lines of "a kind of movement pattern" (see Christensen & Jola 2015, p. 230; for a critical review of dance in scientific studies, see Jola, Ehrenberg & Reynolds 2012), suggestions on how functional changes related to dancers' mirror neuron system activity can be linked to their health and wellbeing are hitherto limited.

An interesting aspect of functional brain imaging studies and dancers' health and wellbeing not yet discussed relates to dancing in synchrony with a partner or to a beat, that potentially acts as a mood enhancer. For example, several studies found that pro-social behaviour is enhanced through moving in synchrony (Reddish et al 2013; Hove & Risen 2009; Wiltermuth & Heath 2009; see also review Keller et al. 2014). More specifically, Kokal et al. (2011) showed that drumming in synchrony enhances brain activity in areas that are active in reward contexts (i.e., caudate nucleus, see Figure 3) and facilitates future pro-social behaviour.

Since the seminal study by Hasson et al. (2004) on the synchronisation of spectators' brain activity while watching parts of the feature film "the good the bad and the ugly", methods to analyse neuronal synchronisation across a group of spectators have advanced notably. For example, a group of novice spectators watching Indian dance in the scanner showed a wider network of brain areas synchronised when the music that accompanied the dance moves was audible (Jola et al. 2013). While the authors suggested that the increased synchronisation is based on enhanced shared understanding of the movements by means of coherent multi-sensory stimulation (vision and audition), the exact source for increased synchronisation when audio-visual stimulation in dance is combined could not be identified in this particular study. However, it encouraged a number of following publications that suggested activity in inferior frontal areas, also known for language production, to be enhanced through shared perceived boundaries of complex edited dance movement (e.g., Noble et al. 2014; Herbec et al. under review).

Finally, spectators' resonance with a dance style was suggested to be affected by the narrative (Jola et al. 2011), the live presence of the performers (Jola & Grosbras 2012) and their personality (Jola et al. 2014). Moreover, resources of cognition and emotion potentially compete when watching dance (Grosbras et al. 2012). Hence, dance may simply take your mind off other things and thus improve your health and wellbeing.

In conclusion, although we have learned considerably about modifiers of action observation processes over the last ten years (physical and visual experience, presence of the performer, complexity of dance structure), the links between functional brain processes and dancers' health and wellbeing are yet largely unexplored.

Structural changes – Expertise: Specificity and Efficiency

A close link between structural brain changes and health and wellbeing of an individual has been shown in both directions, positive (e.g., changes leading to enhanced health and wellbeing) and negative (e.g., changes leading to decreased health and wellbeing). Evident cause-and-effect relationships between structural brain changes and wellbeing are examples of brain lesions (i.e., damages to brain tissue) that significantly impact on an individual's health. For example, lesions by injury (e.g., stroke) or infections (e.g., multiples sclerosis, cerebral palsy) have significant effects on the individuals' motor control ability. Alzheimer and dementia are examples of disorders with detrimental effects on health and wellbeing that are accompanied by structural brain changes (i.e., progressive loss of specific neuronal populations). Furthermore, ageing, with its evidently detrimental effects on health and wellbeing was found to be related with reduced grey matter thickness and white matter signalling across sensory, somatosensory, and motor lobes, as well as in parts of the frontal lobe (Salat et al. 2009).

Although structural deterioration is directly linked to a decline in health and wellbeing as indicated above, the causing effects are often unknown. Moreover, the cognitive, sensory and motor functioning in the elderly are not necessarily impaired as a result of these structural brain changes. On the plus side, it is well known that acquiring new skills prompts positive structural and functional brain changes. Notably, physical activity in the form of sporting or musical expertise (Chang 2014) as well as physical intervention (Draganski et al. 2004) repeatedly showed increased grey matter volume in the areas of the trained activity, suggesting motor-training induced neuroplasticity. While most research on neuroplasticity compared experts with novices in cross-sectional studies, longitudinal studies that measure the effect of training over time showed evidence that neuroplasticity is not only fast and efficient but that even low-to-moderate leisure activity can evoke structural improvement (e.g., Bezzola et al. 2012). Research on structural changes in dancers' brains is however unfortunately sparse and less conclusive (Chang 2014).

To our knowledge, only two studies have yet specifically investigated structural plasticity through dance training. Hänggi et al. (2010) compared white and grey matter volume and fractial anisotropy (FA) between professional ballet dancers and non-dancers. FA is a measure of diffusion (directionality of transfer of material, such as water molecules) from one spatial location to other locations over time, thought to vary with fibre density as well as myelination of axons, but is yet poorly understood (Hänggi et al. 2010). Contradicting with a number of studies which showed a correlation between brain volume and physical expertise, the authors reported decreased GM and WM volume as well as decreased FA in dancers compared to non-dancers. While the interpretation of the latter is confined to speculations based on the lack of knowledge on the modifying mechanisms, the decreased GM and WM volume is surprising. Hänggi et al. (2010) provided a number of potential explanations, one of which is the model of expertise efficiency. The idea is that “the higher the expertise, the more efficient the neuronal processing”, which is based on the observation of decreased neuronal activity in experts’ action execution and interpreted as a functional outcome of optimization of the underlying neuronal mechanisms (see Chang 2014). However, as acknowledged by Hänggi et al. (2010), the interpretation does not resonate with a number of findings. Notably, it is inconsistent with the assumptions of the mirror neuron theory and the increased activity measured during experts’ action observation. Other suggestions given by the authors refer to the significant differences in dancers’ weight and years of education. In fact, the latter relates to an earlier observation by Jola and Mast (2008). The authors noted that dancers compared to the control group had reduced levels of higher education (HE) and minimal computer experience, which potentially affected their mental rotation test scores. Hence, when comparing dancers as experts with a control group, rigorous control for potential cofounding variables is crucial.

The second study which compared dancers’ GM volume with that of non-dancers, controlled indeed for computer experience (Hüfner et al. 2011). In contrast to controls, the experts showed decreased GM volume of the anterior parts of the hippocampal formation (see Hippocampus in Figure 3); however, they also showed increased GM volume of the posterior parts of the hippocampal formation and in several other areas in the frontal, temporal, and occipital lobes and the cerebellum. Although explanations of the functional specificity for all of the areas with significant volume differences between experts and novices can be given, the hippocampal formation was of particular interest for the authors due to its involvement in vestibulo-visual stimulation, navigation, and memory. While this study controlled well for confounding factors as well as effects of expertise with a number of additional tests, it is not clear which brain differences are specific for dance, as also ice dancers and slackliners were included in this study.

More research is needed into how dancing experience leads to structural brain changes in order to advance both direct and indirect neuronal exploratory mechanisms on the dancing benefit for individuals' health and wellbeing. Further studies are needed that control for different levels of intellectual abilities and different physical demands, such as cardiovascular activity, across the range of dance styles. Finally, a major criticism of most studies on motor-induced neuroplasticity is that the special skills acquired are often only defined on a descriptive qualitative basis. It is not unlikely that they are expressed post-hoc, following the identification of brain areas with significant changes instead of a theoretically based approach.

Psychosocial mechanisms

A variety of psychosocial factors that may justify the benefits of physical activity in wellbeing have been reported (Buckworth et al. 2013): increased perceived competence, control of own body or physical appearance, increased perception of autonomy and self-acceptance, affiliation and belonging through improved social contact are likely to impact individuals' self-concept and self-esteem. In dance, these elements were often identified as beneficial factors (Quiroga Murcia et al. 2010) but sometimes as detrimental (Aalten 2007). Therefore, we summarise the psychosocial mechanisms in body image and self-perceptions, mastery and perceived competence, and social affiliation.

Body image and other self-perceptions

Body image is a psychological construct that represents the "individual's perceptions, feelings and thoughts about one's body and incorporates body size estimation, evaluation of body attractiveness, and emotions associated with body shape and size” (Burgess et al. 2006, p. 57). Negative body image has been associated with low self-esteem, obesity, depressive states and other clinical conditions (e.g., eating disorders, social physique anxiety) (Hausenblas & Fallon 2006). Burkhardt and Brennan’s systematic review (2012) showed limited effects on self-concept and body image of children and adolescents’ participation in recreational dance. Connolly et al. (2011) observed significant increases in self-esteem in adolescent girls in response to contemporary dance classes. Notably, attitudes and intrinsic motivation were initially high, indicating that dance is a promising avenue to promote active lifestyles, at least among females. However, the lack of a control group undermines validity of the results. In a methodologically stronger study, Burgess et al. (2006) reported that involvement in bi-weekly aerobic dance sessions for six weeks significantly reduced body image dissatisfaction and enhanced physical self-worth in female adolescents compared to swimming sessions in physical education classes. Specifically, self-perceptions of attractiveness, physical self-worth, feeling less fat and fit significantly improved after the aerobic dance class. The authors point out that aerobic dance may be particularly suited to promote psychological benefits in young girls, predominantly in those who have low levels of self-esteem (Biddle & Mutrie 2008). Other studies (e.g., Aşçi et al. 1998) failed to find significant differences in self-perceptions after an aerobic dance programme in college-aged women, which may indicate an age moderating effect. However, Burkhardt and Brennan’s (2012) meta-analysis provides limited evidence that dance may improve self-concept and body image in dancers aged 5 to 21 years old. In a systematic review on effects of dance intervention in cancer patients, Bradt et al. (2015) also failed to find positive improvements on body image. These controversy results may be due to developmental differences in the participants as well as the level to which dance participants rely on dancing for self-definition (Quiroga Murcia et al. 2010; Padham & Aujla 2007).

Mastery experiences and perceptions of competence

Another mechanism that can explain the effects of physical activity (and dance) on wellbeing is the mastery hypothesis. According to this hypothesis, the successful completion of a challenging and personally meaningful task brings about feelings of accomplishment and mastery (Biddle & Mutrie 2008). Considering the performing context of dance, particularly at the professional level, challenging tasks are required for dancers to achieve a degree of excellence. Therefore, it is not surprising that risk-taking is one of the sought features of contemporary dancers, as Dummont (2012) illustrated.

Grounded on Bandura's (1997) self-efficacy theory, regardless of the level of the dancer, promoting mastery experiences will increase participants' self-efficacy which in turn influences participants' choice of task, perseverance in task completion and positive affective states (Bartholomew & Miller 2002). Bartholomew and Miller (2002) demonstrated that participation in aerobic dance classes resulted in increased positive affect and vigour and in decreases in negative affect, tension and tiredness. However, those who rated their performance as "high" reported greater increase in positive affect 5 and 20 minutes after the class than did those who rated their performance as "low", indicating that a mastery experience may have moderated the experience of positive affective states. Based on the knowledge that high challenges are an important aspect of dance for contemporary performers (Dummont 2012), the dynamic interplay of personal achievements and dance participants' health and wellbeing becomes apparent.

Haboush et al. (2006) found support for increase in self-efficacy and decrease in hopelessness as an outcome to a programme of ballroom dancing in depressed older adults compared to a group on a waiting list. It is thought that the ability to successfully master a particular task brings about positive emotional changes. Another dance intervention with middle-aged psychiatric patients resulted in reductions of depression compared to two control groups (music-only and an exercise-only). Increases in vitality compared to the music-only group were further observed (Koch et al. 2007). In line with suggestions concerning general physical activity (e.g., Matos et al. 2009), dance/movement therapy, a psychological intervention that uses dance and movement as a way of exploring personal difficulties and relationships, can be an adjunct for the treatment of depression (Cruz & Sabers 1998; but see Meekums et al. 2012).

Social Affiliation

One important element of dance is the social bonding, based through touch and so-called entrainment. "Entrainment" is a spontaneous synchronisation to the rhythm of others and is present in humans and animals (Phillips-Silver et al. 2010). It can be found in response to music and movement, while participating in dance (in the form of external, motor synchronisation) or while watching dance (in the form internal, sensory synchronisation). Entrainment provides a strong sense of presence, liveness, and connectedness (Jola & Grosbras 2013) and thus potentially enhances psychosocial wellbeing through dance (Quiroga Murcia et al. 2010). Hence, entrainment may have a positive effect on wellbeing as it may contribute to the fulfilment of individuals' basic psychological need of affiliation (amongst competence and autonomy) (Ryan & Deci 2000). Research is needed to explore this mechanism.

It has been argued that certain types of dance have the potential to improve participants' sense of connectedness (Burgess et al. 2006; Quested et al. 2011; Quiroga Murcia et al. 2010). In a participatory phenomenological study, Cook and Ledger (2004) reported that adult female participants in 5 rhythms dance programme experienced a sense of social connection and belonging while experiencing a safe place where they could express themselves. However, these improvements were not sustained after termination of the programme. These results are consistent with literature in the physical activity domain (e.g. Biddle & Mutrie 2008), suggesting that long-term interventions are necessary.

The positive effects of dance on psychosocial health were also demonstrated in non-clinical and clinical populations in the elderly. For example, Mavrovouniotis et al. (2010) have demonstrated that 60-91 year olds experienced reductions of anxiety and psychological distress after one session of Greek traditional dances, compared to a group who discussed and watched TV for one hour. Kluge et al. (2012) further conveyed that women who were recently relocated to a care retirement community reported more social connectivity, realized they had found a new and improved self, and reported improved mobility. It appears that dance participation promoted personal growth and decreased stress associated with relocation.

Guzmán-García et al.’s (2013) meta-analysis has shown some evidence of increased social interaction and enjoyment among care home residents with dementia and care staff. Specifically, decreases in problematic behaviours, enhancing mood, cognition, communication and socialising after the dancing session were observed. Recent Cochrane Reviews on dance movement therapy also suggests that there are some positive effects of this dance-based intervention for clients with dementia (Karkou & Meekums 2016) or schizophrenia (Ren & Xia 2013). Notably, this research is afflicted with methodological limitations, small sample sizes and an overall small number of studies with randomised controlled trial design.

Conclusion

Dance has gained increased recognition as a form of physical activity with considerable benefits for health and wellbeing. However, research specifically conducted on psychosocial wellbeing in dance is limited compared to research on physical activity and exercise. Although it is reasonable to expect that some mechanisms are shared between dance and physical activity/exercise contexts, it is also reasonable to explore the uniqueness of dance as a creative and performance-related activity. Therefore, there is a need to engage with the different demands of different dance styles, separate recreational dance from elite or vocational dance contexts, and take a developmental approach by considering different elements according to age groups (Burkhardt & Brennan 2012) or other personal characteristics not discussed here (e.g., gender, social status, race). Unfortunately, research focusing on public and leisure settings is scarcer than research in clinical settings (Cook & Ledger 2004), which suggests the need to focus on the different communities within a broader health promotion agenda. Such knowledge would improve the level of consultations on dance intervention programmes allowing better identification of target groups, precision of optimal intervention designs and provide a framework for predictable and testable intervention strategies.

For example, based on literature on music and movement, we found that dance with interactive, live music provides feedback that also increases levels of endorphins more than dance without live music. Moreover, we showed on the basis of recent research on functional brain activity that watching dance with music enhances spectators' brain synchronicity and has significant effects on the enjoyment of the spectators. We outlined the current understanding of social cohesion further supports that entrainment (synchronisation of movement and music) is a hugely relevant factor for successful intervention strategies, in particular when working with groups and the elderly. Hence, explanatory mechanisms for the effect of dance with music are prevalent in all, neuronal, psychological, and biochemical areas.

Further, in order to better support dance intervention programmes, it is essential to understand the level of cardiovascular intensity of different types of dance forms. As outlined, cardiovascular intensity is related to levels of endorphins and cortisol, which need to be known in order to activate the intended health and wellbeing changes related for example to unacknowledged nutritional needs (e.g., due to aesthetic demands, and/or appetite suppression) as well as increased risks of injury (e.g., continuous training despite injury or fatigue).

Researchers should also determine a dose-response relationship in relation to the proposed mechanisms and examine how the different mechanisms interact in the context of dance to promote wellbeing (Buckworth et al. 2013). For example, few authors have measured changes in the brain alongside physiological changes in the body. We believe that in the near future, interdisciplinary research will further advance and that studies combining structural changes and functional brain activity with physiological and psychosocial measures will increase. Such approaches would allow us to more closely relate subjective health and wellbeing with objective brain measures.

To conclude, hopefully, we have clarified the importance of the interplay of the brain and the body when considering health and wellbeing effects in response to dance. Moreover, we believe that this is the first condense review that gave dance-related processes on the outer cortical surface as well as the inner brain structures equal attention. We anticipate that the increasing presence of dance in science will further signify the value of dance as an embodied art form and evidence its benefits on recreational as well as professional level as a form physical practice that includes further psychosocial and artistic aspects worth practicing and researching (Giersdorf 2009).

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Figure Legends.

Figure 1: An elderly couple dancing. Dance is not restricted to age, gender, or physical appearances and dance intervention benefits can be found on a wide age-range. In fact, while age as an indicator of physical maturity should be taken into consideration for the outline of appropriate training, encouragement that performing and enjoying dance is possible at a higher age and that training can start late is plentiful. Figure by Rebecca Leith.

Figure 2: The hypothalamic-pituitary-adrenal (HPA) axis that regulates the stress response of an organism through the production of the hormone corticotropin releasing factor (CRF) in the pituitary gland is illustrated above. CRF liberates the adrenocorticotropic hormone (ACTH) which in turn, the ACTH acts on the adrenal glands liberating a number of hormones onto the blood stream, including mineralocorticoids (mainly aldosterone), and glucocorticoids (such as cortisone, corticosterone and, most importantly in humans, cortisol). A small fraction of these glucocorticoids remains “free” in the blood stream (i.e., unbounded to chemical substances) and is eventually diffused to the saliva (Rohleder, Beulen, Chen, Wolf, & Kirschbaum, 2007). The main goal of the HPA system is to prepare the organism for an efficient “fight or flight” response to a stressor and to protect against long-term stress. An excessive activation of this system induces biochemical alterations, which interfere with the functioning of brain structures that regulate the emotional states, such as the amygdala, the hippocampus and the nucleus accumbens (O’Neal et al., 2000). Therefore, low levels of cortisol are a biomarker of good health (Miller, Chen, & Cole, 2009). Figure by Rebecca Leith

Figure 3: Internal structures (right side) and outer cortical surface from the lateral (side-) view (left side). Indicated are the four main lobes of the cortex (outer layer of neural tissue, i.e., grey matter/cell bodies), areas considered part of the mirror neuron network (i.e., primary motor cortex, the inferior frontal gyrus, the inferior and superior parietal lobe, the superior temporal sulcus, and the somatosensory cortex) and internal structures associated with relevant biochemical mechanisms. Figure by Rebecca Leith